

A RECLASSIFICATION OF THE ORDER ODONATA.

BASED ON SOME NEW INTERPRETATIONS OF THE VENATION
OF THE DRAGONFLY WING.

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CONTINUATION THEREOF.

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PART II.

The Suborders Zygoptera (continued), and Protanisoptera.

In this Part we take leave of the Coenagriodea and, in doing so, note that they had attained to a stage of evolution in the Upper Permian which has remained practically static from then until the present day.

From the main stem of this superfamily, and most probably, from the Lestid complex, an important branch was thrown off, the *Megapodagriidae*. At what geological horizon this occurred it is difficult to say, but as the *Amphipterygidae*, which have descended from them were well advanced in the Jurassic, we may safely conclude that the *Megapodagriidae* originated early in the Triassic; the fossil record for the Odonata at this horizon is however entirely negative.

Because of this absence of fossil evidence, we are compelled to seek for the probable ancestors among the archaic forms which still exist today, and in doing so it is important to bear in mind the chief characters which separate the wings of the higher forms from those of the Coenagriodea. In general, we note a marked advance in the type of venation; the system of cross-veins has greatly increased and, for the first time, we note that the two primitive antenodals no longer stand alone. The whole strength of the wing appears to have been dependent on a soundly built costal-antenodal complex from which the rest of the structures of the wing could be slung. The two primary antenodals appeared very early as an ordinal character in the venation of the Odonate wing, and along with the cross-nervure *Ac*, which has been fixed by the anal tracheal crossing, they have blazed a trail through the evolutionary history of the wing which it is necessary we should follow if we are to arrive at a correct interpretation of that history. I shall therefore devote a little time to the study of the primaries in the various families. (Fig. 1, A to G.)

The earliest appearance of the primary antenodal nervures, which have been termed by other authors—the “strong antenodals”—to distinguish them from the more weakly constituted “secondaries”, is in the Protozygoptera of the Lower Permian. In *Sushkinia*, *Progoneura* and probably also in *Opter* (which is so poorly preserved that these nervures cannot be made out) we find the primaries in a very primitive condition; the costal and subcostal halves are approaching one another but have not yet come into alignment. They are two in number and are unaccompanied by any secondaries, save in *Progoneura*, where there is a single costal antenodal distal to the primaries. In *Kennedyia* and also in *Permagrion*, which is an annectant genus lying between the Protozygoptera and Zygoptera, evolution has gone forward and the two constituent halves of the primaries are now in alignment. From now onwards, throughout the whole Order

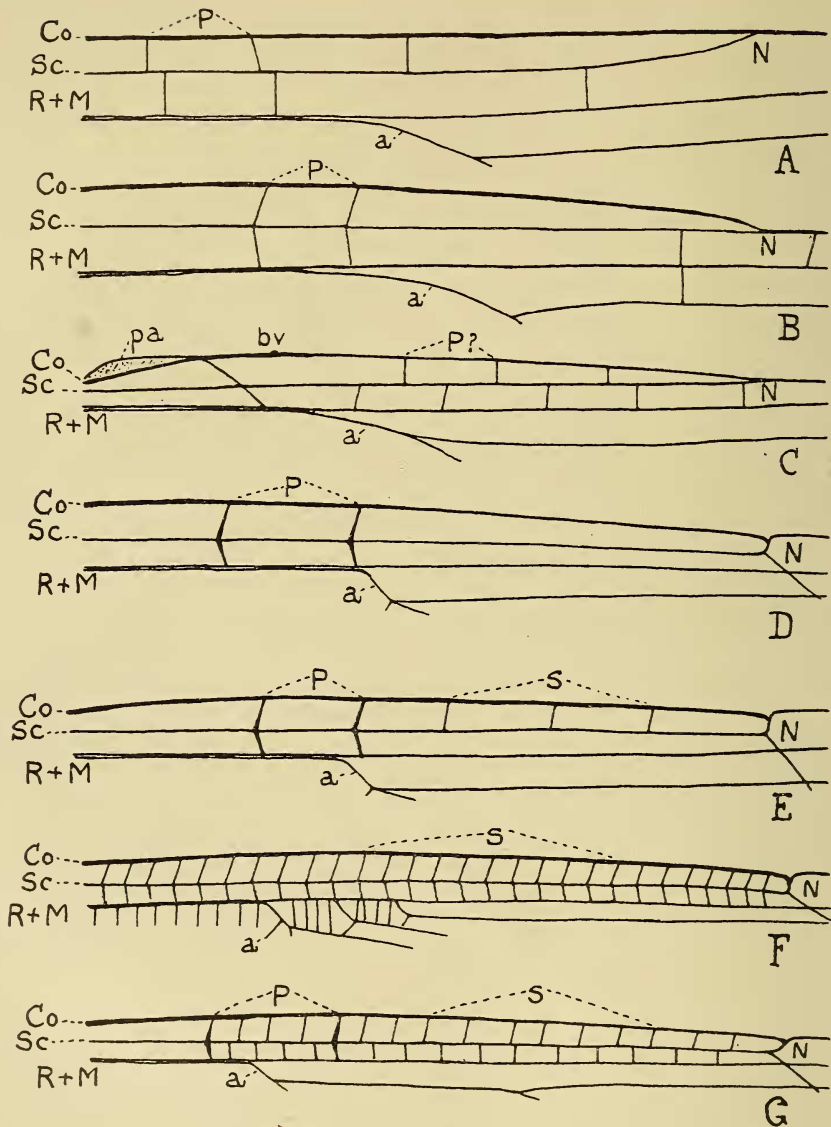


Fig. 1.—Evolution of the Costo-antenodal complex:—A.—Costal and subcostal antenodals not coinciding (*Progoneura* Carp., Protozygoptera). B.—Costal and subcostal antenodals now in alignment and forming the two primary antenodals (*Kennedyia* Till., Protozygoptera). C.—Possible formation of primary antenodals in *Ditaxineura* Till. (Protanisoptera). D.—The primary antenodals completed (Coenagriioidea). E.—Secondary antenodals now present in the costal space, reinforcing the primaries (Amphipterygidae).

F.—Secondary antenodals in both costal and subcostal spaces and all in alignment. The primaries, at this stage, become obsolete (Agriidae). G.—Secondary antenodals in both spaces but not coinciding; primaries still present (*Epiophlebia* (Selys), Anisozygoptera). P., Primaries; N., Nodus; a, Arculus; bv, Brace vein; S, Secondaries; pa, Precostal area; Co, Costa; Sc, Subcosta; R + M, Radius plus Media.

Odonata, save in the most recent families, where their presence is concealed, the primaries exist as an ordinal character. More especially, we must note that *the proximal primary antenodal is the most basal of all the antenodals*, save in some very recent genera and species.

In the Protanisoptera, which will be more fully described below, we meet with a condition of the antenodal complex which is quite unique in the Order. From the apex of the precostal area an oblique vein runs distalwards, crossing the subcosta to meet the combined Radius and Media. (Fig. 1, C, bv.) It is analogous, if not homologous to the same oblique vein found in the Plectoptera. Both Dr. Tillyard and Professor Carpenter have fallen into the error of confusing this vein with the proximal primary antenodal, which it cannot possibly be, since the latter is never connected with the base of the wing and always situated well distal of it; moreover it is too oblique and shows no evidence of ever having been constructed from separate costal and subcostal portions. It has no analogy with the proximal primary found in the Protozygoptera and in the rest of the Order Odonata. In *Ditaxineura*, this oblique vein is followed, some way distally, by two costal antenodals and three subcostals, all spaced rather widely and alternating with each other at about equal distances. One or more antenodals are seen more distally but too far out indeed to take any part in forming the primaries. The primaries may, however, be developed later by a gradual coincidence of the two more proximal pairs? But if this did eventually take place, then we should expect to find them perfectly aligned in the much more highly developed *Polytaxineura* and *Pholidoptilon*. In the former, the 5th and 6th antenodals are aligned but appear to be no more highly differentiated than the rest; their alignment may be purely accidental as often happens when a great number of antenodals exist in either space, as is the case in *Polytaxineura*. In *Pholidoptilon* only one set are in alignment and these too far out to be the distal primary antenodal. It seems clear then that the primaries are altogether absent in the Protanisoptera, and that the absence of this important ordinal character stamps them as, not only a very early offshoot from the root of the Odonata, but, at the same time, altogether precludes the possibility of their being the ancestors of the Anisozygoptera and Anisoptera. Additional proof of this will be given when dealing with the Protanisoptera below.

In the Coenagriidae, the primary antenodals retain the condition found in *Permagrion*, and it is only when we arrive at the *Megapodagriidae* that we first meet with secondary antenodals. In *Trineuragrion*, a single subcostal antenodal is found distal to the primaries, and in *Neurolestes* a complete antenodal is found lying between the primaries.

It is only when we come to the *Amphipterygidae* that we find secondary antenodals supporting the primaries as a *constant* character. At first sight, very little seems to separate this family from the *Megapodagriidae*, but when we come to compare the venation of the two, we find that whereas *the postnodal nervures in the latter are in strict alignment with the cross-veins connecting Ri with Rii, they fail largely to coincide in the Amphipterygidae; this character is constant for the whole of the higher Zygoptera.*

It is convenient here to recall the fact that the postnodals in *Hemiphlebia* do not coincide with the cross-veins between *Ri* and *Rii*, but since it possesses neither intercalated sectors nor secondary antenodals, it cannot be included in either the *Megapodagriidae* or *Amphipterygidae*; its place seems to lie immediately adjacent to these two families in a family of its own, the *Hemiphlebiidae*. I do not think that there is sufficient justification to raise it to superfamily rank.

Dr. Tillyard, following other authors, has placed the two fossil genera *Dysagrion* and *Phenacolestes* in the *Megapodagriidae*, but since, in them, the postnodals fail to coincide with the cross-veins following them posteriorly, I now transfer them to the *Amphipterygidae* along with a number of other fossil genera detailed below under the description of this family. (Fig. 3, 1 to 6.)

In the genus *Philoganga*, belonging to this family, a new type of antenodal first makes its appearance at the extreme base of the wing, proximal to the proximal primary antenodal. (Fig. 4, 1.) These exist in the subcostal space only, but, as we shall see when we come to study more highly developed forms in both the suborders Zygoptera and Anisoptera, they tend to become complete. Along with this, the secondaries, from non-coinciding elements, become aligned to form complete cross-nervures, and when this is completed, the primary pair atrophy and finally disappear altogether. Out of this evolution, we are able to formulate the following axioms:—

- (1) Species with only primary antenodals are more primitive than those with secondaries.
- (2) Species with primary and secondary antenodals are more recent than those with only primaries, but more primitive than those with primary, secondary and additional basal antenodals.
- (3) Species with the whole of the secondary antenodals in alignment and the primaries atrophied or obsolete, are more recent than all others.

These three axioms furnish us with a useful yard-stick with which to appraise the age and placing of any particular species, genus or family.

We may now resume the review of the general venation of the higher forms, and first, we notice that an important character is the formation of a number of intercalated veins or sectors between the distal parts of the main veins. This is already in evidence in the *Megapodagriidae*, but is further augmented in the *Amphipterygidae*. It is well illustrated in *Diphlebia* (Australia) and reaches its culmination in *Neurobasis* (Australia) of the Agriidae. (Fig. 4, 3 and Fig. 8.)

Of greater interest, from an evolutionary point of view, is the almost static arrangement of the branches of *Rs*. In the older Zygopterous types we noticed how the course of evolution was characterized by a progressive movement of the origins of these branches towards the base of the wing, culminating in the Lestid type in which both *Riv* + *v* and *IRiii* arise close together and considerably nearer to the arculus than to the nodus. This Lestid condition for the origins of these two veins is *basic for the whole of the higher families of the Odonata, both in the Zygoptera and Anisoptera*. It will be seen to be attained in the Amphipterygid genus *Diphlebia* (Australia) and is so for the whole of this family, although not quite complete in *Philoganga* (Oriental). The conclusion at once suggests itself that the immediate ancestor of all the higher forms was one in which the

Lestid position of the origins of *Riv + v* and *IRiii* was well in process of attainment.

In the *Amphipterygidae*, we see therefore, clear cut links connecting the Coenagriodea with the higher Zygoptera and Anisoptera.

From the *Amphipterygidae* arose a number of branches from which, ultimately, were developed the higher forms of the Zygoptera and the new suborder Anisozygoptera. It is probable that these branches were multiple and widely divergent in character, for the five primitive genera which have survived up to the present day differ to a remarkable degree, although agreeing in the fundamental characters of the costo-antenodal complex, proximal origins of the *Riv + v* and *IRiii* and the intercalated sectors.

Within the superfamily Agrioidea, which includes all the Zygopterous families from the Amphipterygidae upwards, there is no approach in the shape of the discoidal cell to the acute distal angle found in the Lestid complex, so that we are driven to search for ancestral types somewhere within the complex of ancient forms included under the family *Megapodagriidae*. Of these, the genus which most closely approaches the ideal is *Rhipidolestes*, in which the origins of *Riv + v* and *IRiii* have already attained much the same position as in *Philoganga* (*Amphipterygidae*), while the general arrangement of all the other main veins is closely similar and the discoidal cell is of the shape required in the ancestral form of the Agrioidea. But in *Rhipidolestes* the postnodals are in alignment with the adjacent cross-veins, a character quite unknown in the Agrioidea. We have therefore still to find a type possessing those features common to *Rhipidolestes*, but with the postnodals out of alignment with their neighbouring cross-veins. Such annectent forms are those of *Pseudolestes*, *Petrolestes*, *Phenacolestes*, etc., which bridge the gap between the Megapodagriidae and Amphipterygidae. *Pseudolestes mirabilis* Kirby, in its forewing, possesses all the characters necessary for the ancestral type of the Agrioidea. Thus I consider that a clear case has been made out for the evolution of this superfamily from a Megapodagriine ancestor related to *Rhipidolestes*, and an Amphipterygine one not far removed from *Pseudolestes*. (Fig. 2, 1 and 2.)

The evolution of the Anisozygoptera offers no such difficulty in the matter of the shape of the discoidal cell, since in all the genera, this cell,

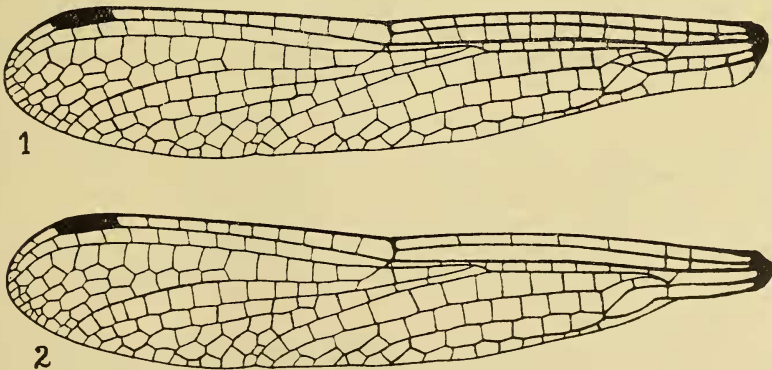


Fig. 2.—1.—*Pseudolestes mirabilis* Kirby. 2.—*Rhipidolestes aculeata* Ris.

in the forewing at least, is of a distinctly primitive Zygopterous shape. This suborder will be dealt with more fully in Part III.

A further point of interest in the evolution of the Agriodea is the structure of the arculus and the main veins arising from it. If we compare this region in a primitive genus such as *Diphlebia* (Fig. 4, 3), with that of *Austrolestes* (Fig. 18, Part I), we see that the general arrangement, including not only the positions of the origins of Riv + v and IRiii, but also their direction in relation to one another, are the same in both, the only important differences (apart from the shape of the discoidal cell) lie in the presence of a few secondary antenodals in *Diphlebia*, and in the more centralized position of the nodus, which increases its relative distance from the arculus. But in the higher types of the superfamily, two remarkable lines of evolution became manifest, neither of which has any counterpart in the other families of the Zygoptera.

The first of these two developments is that found in the family Polythoridae (Fig. 6, 2), confined to S. America, and consists of a recession of the short common stem of Rs + MA (or anterior arculus) right back to the Radius itself, so that the arculus becomes obsolete and the base of the discoidal cell becomes suspended, as it were, from the distal primary antenodal. Now in most of the genera belonging to this family, the proximal primary antenodal has disappeared; it is clear then that the distal one has been preserved to take the pull of the attachment of the discoidal cell; it has, in fact, taken the place of the arculus and is not only preserved but actually thickened and strengthened.

The second line of evolution is one which is not concerned with any change in the form of the arculus itself but begins with a strong anterior-wards arching of the vein Rii + iii, immediately after its origin from Rs. This can be seen in its most elementary stage in the genus *Libellago* (Chlorocyphidae) (Fig. 5, 3) *Rhinocypha tincta* (Queensland)). The next stage is an atrophy of the basal portion of Rii + iii, which, owing to the anterior arching, has come to lie in close proximity to Ri (Fig. 7). The final stage is reached in the highest forms (Fig. 8, *Neurobasis*), by a secondary fusion of the arched Rii + iii with Ri, and this fusion may last so long as to make it appear that both IRiii and Rii + iii have separate origins from Ri; it is only the persistence of the original common anteriorly arched stem from Riv + v as an *oblique vein* which gives us the key to the solution of this venational problem. In some genera and species, even the oblique vein has disappeared, so that without the aid of comparative anatomy, we could not arrive at the solution of the problem.

Throughout the Agriodea, with but few exceptions, the females have preserved largely their primitive condition of uncoloured and similarly shaped fore and hind-wings, in striking contrast to the males whose development has gone ahead and along widely diverging lines. This, of course, has been the outcome of sexual selection, whereby utility or the power of flight has been sacrificed for the sake of appearances. Flight in the primitive Zygoptera is "sculling" in nature, as is well demonstrated in those species with dark banded wings (*Disparoneura quadrimaculata* (Rambur) and *D. apicalis* (Fraser)).

These species have a steady hovering flight and the combination of rapid sculling action of the wings with their dark transverse bands, produces a kinematic effect of dark circles suspended in the air. In the higher Zygopterous forms, the flight of the females is similar to that of

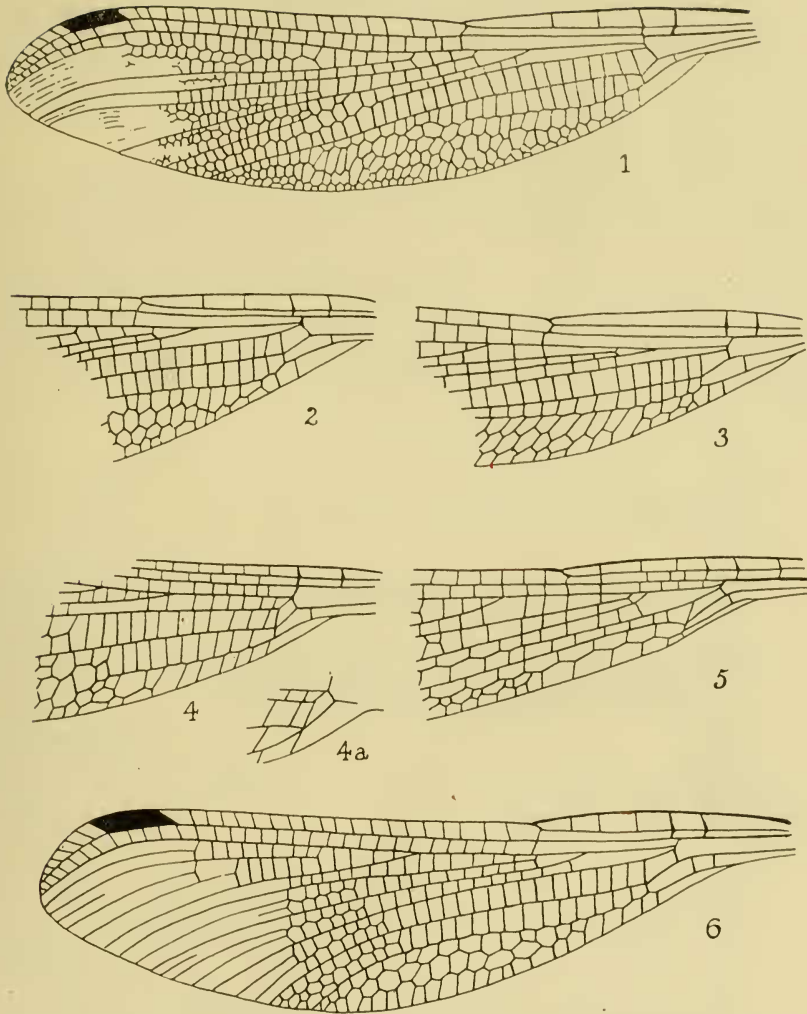


Fig. 3.—Possible ancestral forms of the higher Zygoptera and Anisozygoptera:—1.—*Dysagrion packardi* Scudd. 2.—*Dysagrion fredericci* Scudd. 3.—*Petrolestes* Cock. (Eocene, N. America). 4.—*Triassolestes* Till. (Triassic, Queensland). 5.—*Steleopteron*. Handl. (Jurassic, Bavaria). 6.—*Phenacolestes* Cock. (Miocene, N. America.).

the primitive forms, but in the males, owing to a broadening of the hind-wings and the need to keep these latter as motionless as possible to display their brilliant colouring to the female, flight is a combination of sculling with the forewings, which act as propellers, and planing with the hind-wings. We have frequently observed *Neurobasis chinensis* L. (Queensland)

in the act of pursuing a female, planing closely over the surface of a turbulent stream, rising over the crest of miniature waves and dipping into the trough between them, its forewings hardly visible, so rapidly were they beat, its hind held horizontally outwards with occasional slight alterations in their inclination so as to display their glorious metallic colouring to the best advantage. In this way, sexual selection has had a profound effect on the evolution of the Agrioidea.

In presenting a new classification of the Agrioidea, we shall, as in our previous studies in Part I, make use mainly of the wing-venation. Unfortunately, the larval characters, which would obviously be of the greatest assistance in determining the affinities of some of the more puzzling forms, are only known for a few genera, and hence the placing of such forms as *Devadatta*, *Heliocharis* and *Pentaphlebia* may be considered as still a matter for discussion. Apart from venation, the peculiar structure of the clypeus in the Chlorocyphidae and the great length of the legs in other families appear to be of great importance; lastly the structure of the genitalia is assuming yearly a greater value, as fresh studies are made of these organs.

The following key will serve to distinguish the families:—

1. Both primary antenodal nervures present; arculus present; discoidal cell well separated from Ri. 2.
Both primary antenodal nervures absent; arculus present. 4.
Only the distal primary antenodal present (except in *Euthore* and some species of *Cora*, where both are present); arculus absent. *Polythoridae*.
2. Rii + iii more or less arched towards Ri, shortly after its origin; secondary antenodals numerous. 3.
Rii + iii not arched towards Ri; secondary antenodals few in number. *Amphipterygidae*.
3. Clypeus produced in the form of a prominent snout; no basal antenodals ever present. *Chlorocyphidae*.
Clypeus not produced; nearly always basal; antenodals present. *Heliocharitidae*.
4. Rii + iii not usually fused with Ri, shortly after its origin; anal vein without a recurrent branch; discoidal cell short, usually shorter than basal space and either untraversed or traversed by very few cross-veins *Epallagidae*.
Rii + iii nearly always fused with Ri for a short distance after its origin; anal vein with a recurrent branch or itself recurrent; discoidal cell elongate, usually as long as basal space and traversed by numerous cross-veins. *Agriidae*.

Family 1. AMPHIPTERYGIDAE. (Fig. 4, 1 to 4.)

The *Amphipterygidae* together with the *Megapodagriidae* consist of a number of rather indeterminate genera which bridge the gap between the Coenagriodea and Agrioidea. They differ from the *Megapodagriidae* mainly, by the failure of the postnodal nervures to coincide with those cross-nervures lying between Ri and Rii and by the discoidal cell which, from an acutely pointed quadrilateral, becomes more definitely rectangular. In some genera, however, the discoidal cell is still acutely pointed outwardly, as in *Hypolestes*, etc. Another character, which first appears in the *Megapodagriidae*, although only occasionally, is established as a *constant*

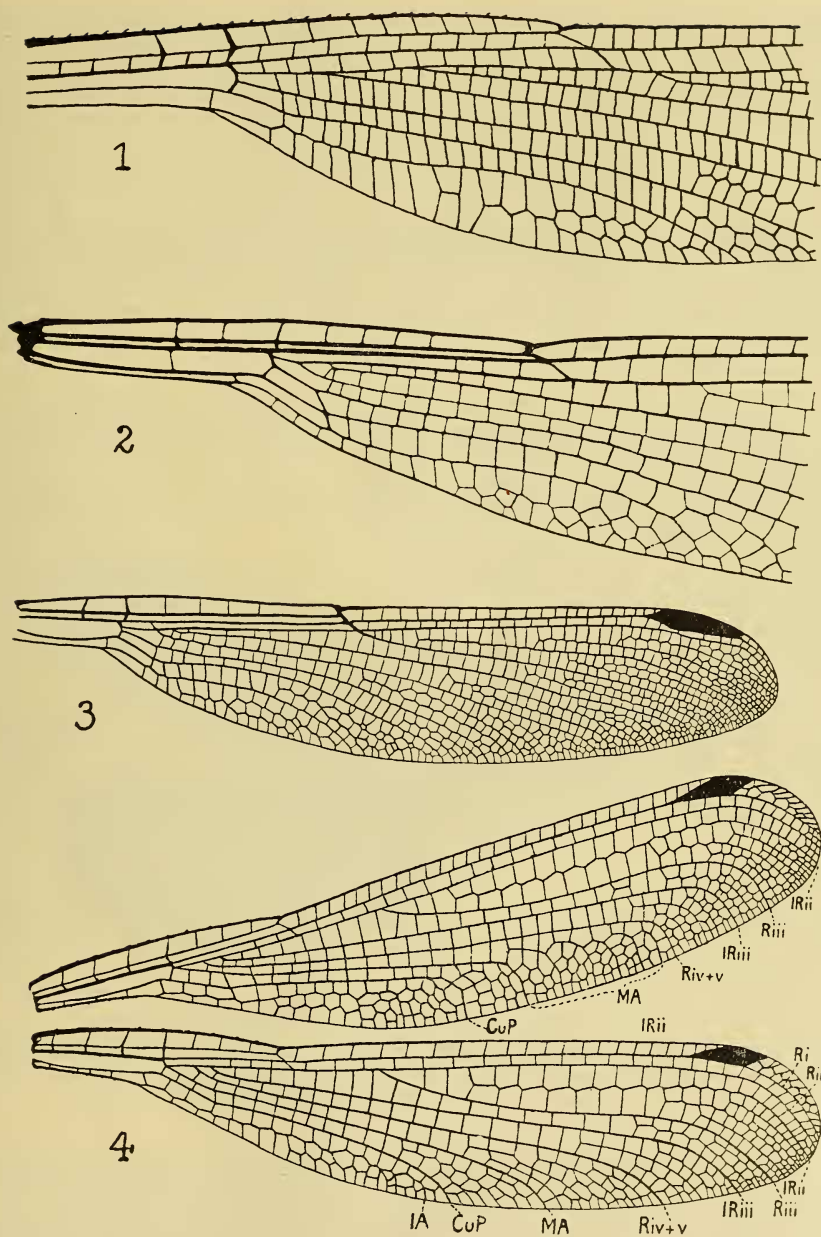


Fig. 4.—Amphipterygidae:—1.—*Philoganga loringae* Fraser (Oriental).
 2.—*Amphipteryx agrioides* Selys (Neotropical). 3.—*Diphlebia
 lestoides* Selys (Australia). 4.—*Devadatta argyoides* (Selys)
 (Oriental).

feature of the wing, viz., the presence of secondary antenodals to augment the primaries. These are usually confined to the costal space and distal to the primaries only. In *Devadatta*, however, the secondaries have extended into the subcostal space and four or five of them are in strict alignment, foreshadowing what we find in the Agridae. The wings are still petiolated to nearly as far as Ac; the discoidal cell is a more or less elongate rectangle or subrectangle, entire or crossed by one or two veinlets as in the Epallagidae; the pterostigma is elongate and strongly chitinized. Of more importance are the first indications of a broadening of the wings as evidenced by a pectinate or wavy branching of the ends of the main veins, more particularly those of CuP and IA. This is strikingly demonstrated in *Devadatta argyroides* (Selys), where the venation of the forewing differs from that of the hind; the distal ends of the main veins of the forewing curve downwards abruptly in a series of waves, whilst those of the hindwing run almost flatly to the border of the wing. (Fig. 4, 4.)

This family contains medium-sized insects of moderate or robust build and having the general appearance of large stoutly built Lestidae; the head, transverse with large, button-like eyes; the thorax robust, abdomen elongate and male anal appendages forcipate. In the position of rest, the wings, in some at least, are held wide open (*Diphlebia* and *Philoganga*) as in the Anisoptera. The only known larvae are those of *Diphlebia* and *Philoganga*, which are remarkably similar, in strong contrast to the perfect insects; they are found clinging to the underside of rocks in torrential streams, are flattened beneath, with short, flat labial mask having narrow lateral lobes without setae and ending in three distal teeth and a long, sharp terminal hook; the caudal gills are saccoid or triquetral and there are no lateral abdominal gills.

Pending the discovery of other larval forms, the relationships of the genera included in this ancient family must remain more or less problematical. The genus *Philoganga* differs more strongly from the rest and therefore merits the erection of a subfamily as has been done by Kennedy. The two subfamilies may be defined as follows:—

Subfam. *Philoganginae* Kennedy.

Subcostal antenodals more numerous than the costals; basal subcostal antenodals invariably present. Origins of Riv + v and IRiii arising rather distally, about midway between arculus and nodus. Discoidal cell short.

Only one genus—*Philoganga* Selys (Oriental).

Subfam. *Amphipteryginae* n. subfam.

Costal secondary antenodals more numerous than the subcostals, which latter are usually absent between the arculus and nodus. Origins of Riv + v and IRiii very close to arculus; discoidal cell elongate.

Genera are both recent and fossiliferous:—

Recent: *Diphlebia* Selys (Australian), *Amphipteryx* Selys Neotropical, *Devadatta* Kirby (Oriental), *Pentaphlebia* Förster (Ethiopian), and *Pseudolestes* Kirby (Oriental). Fossiliferous: *Dysagrion* Scud. (Eocene), *Protamphipteryx* Cock. (Eocene), *Petrolestes* Cock. (Eocene), *Phenacolestes* Cock. (Miocene).

To these, *Hypolestes* also probably belongs if its larva has been determined correctly, although it must be pointed out that the postnodals are in strict alignment with the cross-veins posterior to themselves and this

alone would place the genus in the *Megapodagruidae*. It will be noticed that Dr. Tillyard has placed the two genera *Dysagrion* Scudd., and *Phenacolestes* Cock., in the *Megapodagruidae*, but in both these, the postnodals fail to coincide with the cross-veins behind them, a character which carries them forward to the *Amphipterygidae*. *Dysagrion*, *Phenacolestes*, *Petrolestes*, *Philoanga* and *Diphlebia* form an instructive series demonstrating the gradual recession of the origins of Riv + v and IRiii.

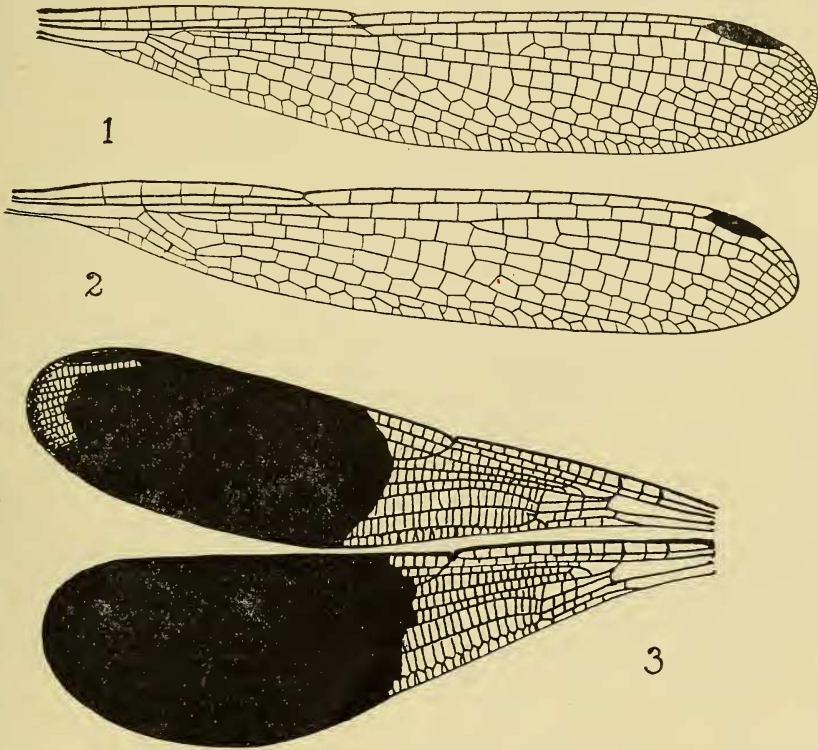


Fig. 5.—Chlorocyphidae:—1.—*Chlorocypha* Fraser (Ethiopian). (Note the anterior arching of Rii + iii). 2.—*Libellago* Selys (Oriental). (Note the absence of the anterior arching of Rii + iii in this primitive genus). 3.—*Rhinocypha tinctoria* Rambur (Australia). (Rii + iii markedly arched.).

Family 2. CHLOROCYPHIDAE Cowley. (Fig. 5, 1 to 3.)

Wings subpetiolate, narrow and similar in shape in the females, narrow or more or less dilated medially, especially the hindwing, in the males. The primary antenodals always present, as well as numerous secondaries, varying from five to twenty. Nodus situated between one-third and half-way along the costa; discoidal cell an elongate rectangle, always traversed; pterostigma narrow, elongate and strongly chitinized. Rii + iii, shortly after leaving Rs, straight in primitive genera, but distinctly arched

anteriorly in all others; IA zigzagged and with a single row of cells behind it. Head very narrow, eyes very large and placed more closely together than in other Zygoptera; clypeus projecting forwards markedly as a kind of snout. Thorax robust, abdomen shorter than wings (except in the aberrant genus *Rhinoneura* Laidlaw, where the abdomen is slender and longer than the wings).

Larvae differing markedly from those of the previous family; head subtriangular, with rather long antennae and strongly projecting front; labial mask with triangular medial lobe, cleft in the middle, the lateral lobes narrow, armed with setae near the base and furnished distally with hooks and sharp teeth. The legs very long and slender; the two lateral caudal gills narrow, horny, triquetral in section and armed with strong spines; the median gill represented only by a stout conical spine (*appendix dorsalis*). Found clinging to drift-wood or floating weeds and submerged roots in montane streams.

From the entire absence of basal antenodals, the persistence of the two primary antenodals and the complete failure of the secondary antenodals to coincide in their costal and subcostal series, we see that this family is one of the most primitive of the Agrioidea and that its origin was from somewhere within the Amphipterygid complex. The earliest forms in the family were undoubtedly close to *Libellago*, in which the antenodal complex is very simple and the vein Rii + iii shows but little sign of the anterior arching which later characterizes the Agrioidea. *Libellago* is purely Oriental in distribution, so that we may safely surmise that this family had its origin in Asia and spread later eastwards to the Pacific, southwards to Oceania, and westwards to Africa.

Two aberrant genera must be noticed, viz., *Rhinoneura* Laidlaw, and *Disparocypha* Ris. The former is characterized by its strongly petiolated wings and long abdomen, which both suggest an origin from a form approaching *Devadatta*, but the forward arching of Rii + iii rules this out. The other genus, *Disparocypha*, which agrees with *Rhinoneura* in the curious shape of its pterostigma, is characterized by a great reduction of the base of the wings. History has repeated itself in this genus, for just as the anal vein, by reduction of the base of the wing, became confluent with the posterior border in the Coenagriodea, so in this genus, by a similar process, the anal vein has become fused with the wing border, along which it can be traced to as far as the first cross-vein below the discoidal cell. It is the only genus in the whole of the superfamily Agrioidea in which the anal vein is so confluent. The slight arching of Rii + iii towards Ri shows that the genus postdates *Libellago* and that it probably arose from the same stem and at about the same time as did *Rhinoneura*. It is to be noted that a remarkable resemblance exists between *Disparocypha* and the interesting and puzzling Australian genus *Lestoidea* Tillyard; thus they agree in the position of the arculus, the shape of the discoidal cell, the number of longitudinal veins, including the intercalaries, and lastly, by the fusion of the anal vein with the posterior border of the wing. Were it not for the almost complete absence of genera belonging to this family in Australia, one would be inclined to see in these similarities, a relationship which links up the Chlorocyphidae with the primitive Coenagriodea.

Only a single genus with a single species is found within Australian limits, viz., *Rhinocypha tincta* Ramb., Queensland and N. Australia. The genera are: *Libellago* Selys, *Rhinoneura* Laid., *Disparocypha* Ris, *Indocypha*

Laid., MS, *Neocypha* Cowley, *Rhinocypha* Ramb., *Chlorocypha* Fras., and *Calocypha* Fras. (*Libellago asiatica* Selys is the genotype of *Neocypha*, and *Libellago asiatica* subspecies *vittata* that of *Indocypha*). All are Oriental save *Chlorocypha* which is Ethiopian.

Family 3. HELIOCHARITIDAE n. fam. (Fig. 6, 1 and 3.)

Wings long and narrow, petiolate nearly to level of arculus or to slightly proximal of the level of the vein Ac. The two primary antenodals present but widely separated by numerous secondary antenodals, which latter are of both series and many coinciding, especially in the hindwing; basal antenodals almost invariably present, these sometimes complete but usually of

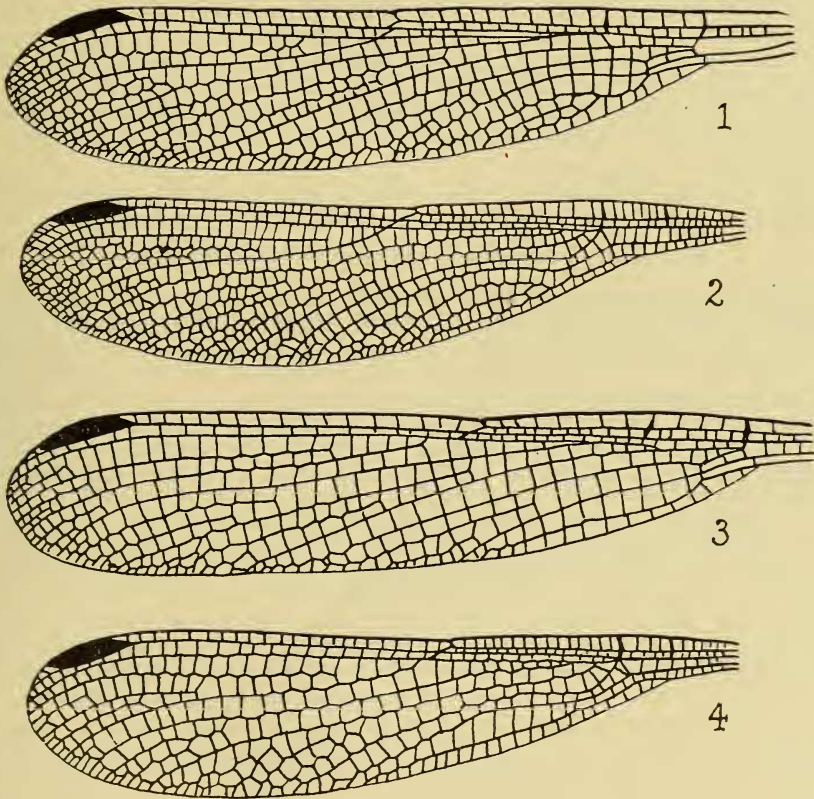


Fig. 6.—Demonstrating the connecting links between the Heliocharitidae and Polythoridae:—1.—*Cyanocharis* Selys.—An advanced type with triadic branching of the anal vein as in the Polythoridae, as shown in—2.—*Cora* Selys. 3.—*Heliocharis* Selys. The anal vein is simple in this genus as in others of the family save *Cyanocharis*. 4.—*Miocora* Calvert.—The most primitive genus of the Polythoridae. Note that it has preserved the simple unbranched condition of the anal vein as in the Heliocharitidae.

the subcostal series only; nodus situated between one-third and half-way along the costa; arculus normal, lying much nearer to base of wing than to nodus and either midway between the primary antenodals or nearest the proximal one; Rs and MA arising normally from about the middle of arculus; Rii + iii arched strongly anteriorly shortly after its origin and thereafter, for a short distance, lying in close contact with or occasionally fused with Ri. Discoidal cell a narrow rectangle, traversed by one or two veinlets; pterostigma elongate, strongly chitinized; IA extending nearly to middle of wing, curving rather abruptly posteriorwards after the level of the discoidal cell, unbranched (except in *Cyanocharis*), area posterior to it undeveloped and narrow; basal space often traversed by several nervures.

This family, which is confined to South America, is evidently derived directly from the Amphipterygidae and from the same stem as *Amphipteryx*, which is the earliest known form to show the basal space traversed, although only occasionally. The family shows an advance on the Amphipterygidae by its shorter petiolation, the greater development of the antenodal complex and the anterior arching of Rii + iii. These characters, the posterior curving of IA and the triadial branching of the same vein seen in *Cyanocharis*, all serve to bridge the gap between the Amphipterygidae and the Polythoridae.

The genera are:—*Heliocharis* Selys, *Dictérias* Selys, *Charitopteryx* Cowley, and *Cyanocharis* Needham. No fossil species are known.

Family 4. POLYTHORIDAE n. fam. (Fig. 6, 2 and 4.)

Wings very variable in shape, petiolate (*Cora*, *Miocora*) or subpetiolate (*Euthore*, *Polythore*, *Chalcopteryx*); both primary antenodals present in *Euthore* and some species of *Cora* (footnote 1) but the proximal one absent in all other genera; secondary antenodals numerous, the two series mainly in alignment, except in *Cora* and *Miocora*; numerous additional basal antenodals present; median space traversed by several veinlets; basal side of discoidal cell produced anteriorly to as far as the Radius, so that the anterior arculus is abolished, and the cell itself is greatly distorted and appears suspended, as it were, from the distal primary antenodal, which latter is compensatingly strengthened and thickened to take the place of the arculus and the pull of the long main veins running from the discoidal cell; Riv + v and IRiii arising close together and close to discoidal cell; both these veins descend from Rii + iii, which continues the lines of Rs and runs almost parallel to the Radius; Rii arising at about the level of the subnodus; IA branching triadically shortly after the level of the discoidal cell, save in *Miocora* where the anal vein is simple as in the Heliocharitidae (but in *Cyanocharis*, IA is triadically branched as in the Polythoridae).

The only known larval form is that of *Cora*, which bears a close resemblance to that of *Euphaea* (Epallagidae); it has saccoid truncated caudal

Footnote 1.—Calvert states that *Miocora* resembles *Cora* in possessing only one primary antenodal (Calvert, 1917, Ent. News, 29: 260), but some species of the latter, viz., *C. modesta* Selys, etc., possess the two, although the proximal one is not nearly as robust as the distal one. It seems evident that he has overlooked the proximal primary in *Miocora* as he has in the case of *Cora*; the venation of the former is so primitive that both primaries must be present. In both genera, the secondaries fail to coincide, a condition which goes with the presence of both primaries. I have not had the opportunity of examining *Miocora* or some of the species of *Cora*.

gills and lateral, so-called, abdominal gills (footnote 2); the labial mask is flat and has two small teeth on the lateral lobes.

This family, as for the last, is confined to the Neotropics, and is undoubtedly a descendant of the Heliocharitidae. The evolutionary connecting links are unmistakable and are as follows:—

1. The two primary antenodals found in the Heliocharitidae are also present in *Euthore* and some species of *Cora* (*C. modesta* Selys) but the proximal one has become obsolete in the more highly developed genera of the Polythoridae.
2. The anal vein is simple and unbranched in the Heliocharitidae, except in the highest developed genus *Cyanocharis* where it is triadically branched. *Miocora* of the Polythoridae has preserved the simple unbranched condition of the anal vein as in the Heliocharitidae, but all other genera of the Polythoridae have the triadic condition found in *Cyanocharis*.
3. In the Heliocharitidae, the stem of Rii + iii runs anteriorly as an *oblique vein* to nearly meet the Radius; in the Polythoridae, owing to the approximation of the discoidal cell to the Radius, and the thereby abolition of the arculus, *this oblique vein has become straightened out* and comes to lie in continuation with Rs and almost parallel to the Radius; Rii + iii still retains its position close to the Radius, as in the Heliocharitidae, the only difference being that its arch has been flattened out.

The genera are:—*Miocora* Calvert, *Cora* Selys, *Euthore* Selys, *Polythore* Calvert and *Chalcopteryx* Selys (Recent), and *Protophore* Cock. (Eocene).

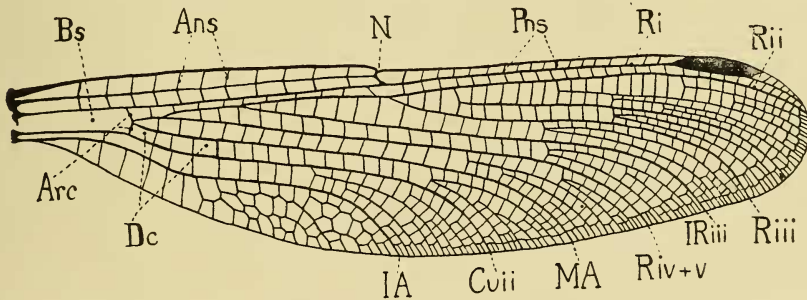


Fig. 7.—*Epallage fatima* Charp., showing the venation of the Epallagidae.

Family 5. EPALLAGIDAE n. fam. (Fig. 7.)

(= *Epallaginae* Fraser, 1928.)

Wings either non-petiolate or very slightly petiolate, the petiolation never extending as far distal as the proximal primary antenodal. Antenodals very numerous and *all in strict alignment*; *primary antenodals both absent*. Basal antenodals numerous and all in alignment (these not

Footnote 2.—The abdominal gills found in certain Zygopterous larvae do not actually function as respiratory organs but are a secondary development and, in fact, pseudopodia, which act as anchoring devices to prevent the larvae being swept away by the swift currents of the streams in which they live.

differentiated from the other antenodals but evidently present as the space between the usual position of the proximal primary antenodal and extreme base of wing, which is normally empty, is completely filled); Nodus near the mid point of costa and situated far out from the arculus; arculus normally present; Rii + iii arching strongly anteriorwards shortly after its origin as in the *Heliocharitidae* but accentuated, this arching bringing Rii + iii either very close to Ri or in actual contact and fusion with it for as far as the origin of IRiii (thus the origin of this vein and Rii + iii appears to be from Ri, while its true origin is indicated by the oblique vein arching up from Riv + v). Discoidal cell rectangular, two to four times as long as wide, entire or traversed by veinlets; pterostigma elongate, strongly chitinized. IA sigmoidally curved; area between it and posterior border of wing filled with several rows of cells distally, these cells separated by more or less complete supplementary veins.

The known larval forms resemble rather closely those of the Amphipterygidae (*Diphlebia* and *Philoganga*), being rather robustly built, with saccoid or triquetral caudal gills and often abdominal gills. The labial mask resembles that of the Amphipterygidae but the distal teeth on the lateral lobe are reduced to two or one. (*Euphaea* has abdominal gills and is found in torrential streams, in which habitats, they serve to anchor the larva to rocks; *Anisopleura* is without these appendages but as they breed in slow water-courses, such as irrigation channels and sluggish streams, the need for them has not arisen.)

This family, which is mainly Oriental in distribution but extends as far westwards as Greece, has no representatives in Australia, nevertheless, its origin was probably in Oceania and from some such Amphipterygid type as *Diphlebia* (Australia). In it we find the antenodal complex reaching its culmination and the whole of the costal and subcostal areas, from base of wing to nodus, are filled with homogeneous synchronized cross-veins. Development of the wing thereafter was confined to broadening it and the adding of numerous intercalated veins and the system of cross-veins and, lastly, to a complicated branching of the anal vein. In the Epallagidae, this development remained almost static in the the case of the females, which have preserved the most primitive type of venation found in the family; thus the females belonging to the different genera are remarkably homogeneous and considerable difficulty is occasionally found in differentiating them. It follows from this, that those genera in which the males most closely resemble the females, are the most primitive. Thus *Epallage* and *Dysphaea ethela*, in which the sexes are undifferentiated save by sexual characters, are the most primitive forms found in the family, and from these we pass to others in which the differentiation becomes ever more wide. Evolution in the males is marked first of all by a tinting of the wings which deepens to a strong amber shade and then becomes infumated and finally opaque; at the same time, there is a gradual broadening of the wings, especially of the hind ones, which are broadened medially and not at the base as in the Anisoptera. The factors bringing about such broad differentiations between the sexes have already been fully discussed above and need not be repeated here.

Genera included in this family are:—*Epallage* Charpentier, *Dysphaea* Selys, *Euphaea* Selys, *Allophaea* Fraser, *Indophaea* Fraser, *Anisophaea* n.nom. (= *Mesophaea* Fraser, preoc.), *Heterophaea* Cowley, *Anisopleura* Selys, *Bayadera* Selys and *Cyclophaea* Ris.

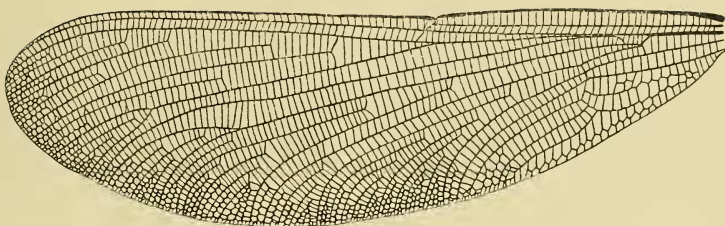


Fig. 8.—*Neurobasis chinensis* L. (Queensland), showing the venation of the Agrididae.

Family 6. AGRIDAE, Tillyard. (Fig. 8.)

Wings non-petiolate, densely reticulated, including, in some genera, the basal space (but this entire in the majority), more or less broadened, the greatest breadth being near the middle of the wings. Nodus from one-third to half-way along the costa; arculus always normal and situated much nearer base of wing than nodus. Antenodal complex complete as in the *Epallagidae*; Rs and MA arising from arculus at or below its centre, or, in the case of the *Hetaerininae*, from its lower part close to CuP. Rii + iii arched as in the *Epallagidae* and usually fused for a short space with Ri. Discoidal cell either an elongate rectangle, very narrow, simply crossed or densely reticulated, or else an irregular quadrilateral with convex anterior side, as in the *Hetaerininae*. Supplementary veins very numerous, straight or more or less strongly curved. The anal vein, IA, which in all previous families forms part of the posterior border of the wing in its basal portion, is, in this family, for the first time, entirely within the wing, and the whole posterior border a simple vein; distally, after the level of the discoidal cell, IA turns obliquely posteriorwards and is then either strongly curved sigmoidally or more or less complexly branched owing to a linking up of some of the numerous supplementary veins developed posterior to it. Usually many additional cross-veins in the cubital space, so that the anal tracheal crossing, *Atc* (= *Ac* Tillyard) is usually obscured (it is isolated and distinct in *Vestalis amoena*). Pterostigma variable, often reduced or entirely absent, especially in the males (in the females, it is usually in a state of atrophy as evidenced by a number of new or additional postnodal veinlets which traverse it; this is usually alluded to as a "false or pseudo" pterostigma, but it would be more correct to call it an "atrophied" one).

This family is made up of a large number of very heterogeneous forms of medium or large size, with head transverse, eyes wide apart, thorax not very robust, abdomen long and slender, and, in the males, always longer than the wings. The superior appendages are forcipate in type. Brilliant metallic colouring of the wings in the males is often found, and this extends to the body and abdomen in both sexes. The larvae are slender bodied with very long antennae, very long, slender legs, cylindrical, slender abdomen and long narrow caudal gills; the labial mask is also long and slender, with deeply cleft median lobe and narrow lateral lobes armed with sharp distal teeth and a long slender movable hook, beneath which setae may or may not be developed. They breed in fast running streams as a rule, and may be found clinging to submerged roots, etc. It is clear that this type of larva is very different from that of the *Epallagidae* and it would appear to be a more specialized development of the type found in the *Chlorocyphidae*. The

origin of the family is probably a very ancient one and from the same Amphipterygid complex which gave rise to the families discussed above; one common character links it to the Chlorocyphidae and Epallagidae, viz., the anterior arching of Rii + iii, but this is absent in the primitive forms of the former, so that we are left with the latter as a possible ancestral line. If the Epallagidae fill this position, then we must explain the broad differentiation between their larvae by the totally different habitats in which they live; we know from other larval forms, that evolution in them has been as great as in the imagines. The culmination of the antenodal complex into a homogeneous unit has been accomplished in the Aagriidae as well as in the Epallagidae. Is this a pure coincidence? or has it been called forth by the same mechanical factors? The latter would seem to be the correct solution since we find it again occurring in the case of the Anisopterous Libellulidae, which can have no near relationship with these two families.

The family is cosmopolitan in distribution but only a single form is found in Australia (*Neurobasis chinensis*). It falls naturally into three sub-families, although I am doubtful as to the relationship of the Hetaerininae. The Aagriinae are found throughout Asia, Africa, Europe and North America, whilst the Hetaerininae are confined almost entirely to South America, their only contact with the *Aagriinae* being by means of a few species of *Hetaerina* with *Agrion* in North America. This terminal and isolated distribution of *Hetaerina* might suggest, at first sight, a derivation from *Agrion*, but the character of their venation entirely precludes such a possibility. For either to arise from the other would entail a complete remoulding of the basal venation of the wings; it certainly could not have been effected by a simple process of reduction or addition to the venation. Thus there seems good reason to believe that the *Hetaerininae* have had an independent origin and have developed along parallel lines to the *Aagriinae*.

Subfamily HETAERININAE n. subfam.

Wings narrow, similarly shaped; discoidal cell strongly curved convexly anteriorwards, its basal side very short; sectors of arculus arising from the lowest part of arculus; basal space always traversed by veins; CuP and IA markedly sigmoidally curved; males with the basal area of wings closely reticulated and coloured with some shade of red and usually with a point of red or black at tips of hind wings; pterostigma usually absent in both sexes.

Genera:—*Hetaerina* Selys, *Mnesareta* Cowley. (Neotropical.)

Subfamily AGRINIENAE n. subfam.

Wings broader than the last, sometimes very broad and variable in shape; discoidal cell a narrow rectangle, with straight anterior side; sectors of arculus arising from middle of arculus; basal space entire or, occasionally traversed; CuP straight; IA variable; males very variable but usually widely different in coloration from the females; pterostigma present or absent, usually present in the females but with veinlets traversing it and markedly atrophied. (Cosmopolitan.)

Genera:—*Agrion* L., *Mnais*, Selys, *Neurobasis* Selys, *Vestalis* Selys, *Matrona* Selys, *Matronoides* Förster, *Echo* Selys, *Climacobasis* Laidlaw, *Psolodesmus* McLachlan, *Archineura* Kirby, *Phaon* Selys, *Sapho* Selys, *Umma* Kirby.

Subfamily CALIPHAEINAE Fraser.

Wings very narrow, similarly shaped, *petiolated* nearly to the level of the anal tracheal crossing; discoidal cell very short, slightly curved anteriorwards, traversed by only one or two veinlets; sectors of arculus arising from just below middle of arculus; basal space entire; CuP and IA straight, the area posterior to the latter totally undeveloped and only one row of cells between it and border of wing; the sexes similar; pterostigma present, a short rhomboid.

Genera:—*Caliphaea* Selys. (Oriental.)

This genus, one of the most puzzling in the Order, is placed in the Agridae on account of the fusion of Rii + iii with Ri and the completely developed antenodal complex. It appears to be an Agrid which has undergone great reduction of the base of the wings, closely paralleling *Disparocypha* of the *Chlorocyphidae* in this respect. Its larva is unknown but the imago occurs in marshes where it has been seen to oviposit; it is the only species of the Agrioidea, I know of, which breeds in stagnant waters.

Suborder 5. PROTANISOPTERA, Carpenter. (Figs. 9 and 10.)

Odonata with moderately broad, non-petiolate wings, the hind only slightly broader than the fore-wings; precostal area present, from the apex of which runs a very oblique, brace vein to descend through the subcosta to the radius; antenodals numbering from 4 to 15 or more, the primaries absent (doubtfully present in *Polytaxineura* Till., Upper Permian, N.S.W.), secondaries numbering from 1 to 12 or more, mostly non-coinciding; postnodals

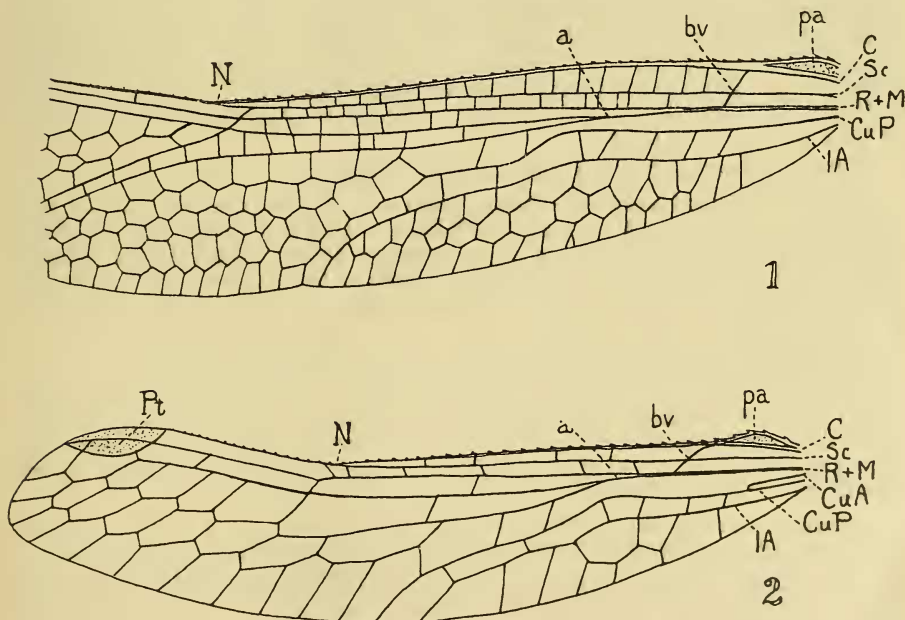


Fig. 9.—1.—*Polytaxineura stanleyi* Till. (Permian of Australia). 2.—*Ditaxineura anomalostigma* Till. (Lower Permian of Kansas).

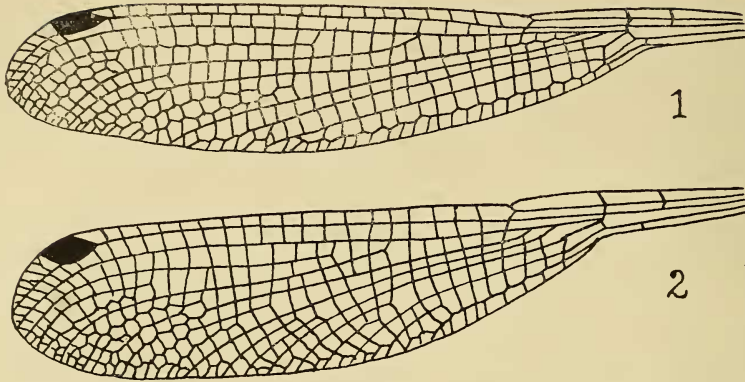


Fig. 10.—Forewing of *Palaeothemis tillyardi* Fraser. In Fig. 2, all the recent additions to the basal and antenodal venation have been removed to show the primitive Zygopterous foundation on which the Anisopterous wing is built. Compare with *Ditaxineura* and *Amphipteryx* (Fig. 4, 3 and 2.).

absent or very few in number; nodus situated distal to the middle of costa, always present and well developed; arculus rudimentary, very oblique; discoidal cell an elongate subquadrangle open at the base in both fore and hind-wings; a rudiment of CuA sometimes present; CuP and IA markedly sinuously curved as in the Meganisoptera, the latter vein always free of the posterior border of wing and arising from its extreme base; anal trachea crossing, Ac, doubtfully present; pterostigma abnormal, bisected by the Radius, broadly fusiform in shape; anal area of wings, posterior to IA made up of 2 to 4 rows of cells.

The Suborder falls naturally into two families:—

Fam. 1. *Ditaxineuridae*.—Basal remnant of CuA present; nodus and subnodus primitive in form; antenodals few, the two series not in alignment except the basal brace vein; postnodals absent; pterostigma broadly fusiform, projecting across radial space nearly to the level of Rii; cross-veins and cells in distal part of wing arranged in two gradate series (as in the *Chrysopa*). (Fig. 10, 2.) 9

One genus:—*Ditaxineura* Tillyard. (Lower Permian, Kansas.)

Fam. 2. *Polytaxineuridae*.—Basal remnant of CuA absent; nodus and subnodus well developed and in line; antenodals numerous and a few in alignment occasionally; postnodals few or absent; pterostigma unknown; cross-veins and cells in distal part of wing not arranged in a gradate series, usually an irregular network. (Fig. 10, 1.) 9

Genera:—*Polytaxineura* Tillyard (Upper Permian, N.S.W.), *Pholidoptilon* Zalessky and *Permaeschna* Martynov (both of Upper Permian of Russia).

Dr. Tillyard states (Proc. Linn. Soc. N.S.W., 1935, 60:375) that the *Ditaxineuridae* foreshadow the *Libelluloidea*, and the *Polytaxineuridae* the *Aeshnoidea* (more open venation, shorter pterostigma, fewer antenodals and postnodals), but it must be pointed out that these characters apply equally well to both superfamilies. The *Polytaxineuridae*, he thinks, lie in

the direct ancestral line of the Anisozygoptera and thereby expresses his whole-hearted belief in Carpenter's theory. This, then, brings us to the most controversial part in the history of the evolution of the Odonata, viz., whether the two major suborders have developed along parallel or serial lines from a common ancestor. This, I think, is best put in the form of the following question:—

“Have the Anisoptera descended from the Protodonata through, or quite independently of, the Zygoptera?”

Whilst there seems to be no doubt that the Anisoptera developed from the Anisozygopterous complex of types, a wide difference of opinion exists among students of the Order as to what was the actual line of descent of the latter. Apart from previous and, now, discarded theories, two hold the field and are best designated by the names of their authors:—

Tillyard's theory.

This theory seeks to explain how the broad base of the Anisopterous wing developed from the narrow, petiolated Zygopterous one by means of recurrent branches thrown off from the stem of the anal vein. Tillyard postulated that the vein IA in both the suborders Anisoptera and Zygoptera was fused at its base with the cubitus, CuP, and that its free condition in the former was only *apparent* and not real. He pointed out that in most primitive forms of Zygoptera, a short vein, which he termed A', could be seen running basalwards from the angle formed by the junction of Ac (*Anal crossing*) and Ab (*Anal bridge*) to the posterior border of the wing. The true course of the anal vein was laid down on its trachea, which could be seen in the larval wing running obliquely up to join CuP and then leaving it by means of Ac, to continue its course along Ab. This was exactly the same reasoning which Comstock and Needham employed to explain the crossing over of Rs, and which Tillyard himself had discredited. The short vein A' was, he said, a recurrent and bridge-like structure designed to connect the anal vein to the broadening base of the wing.

In the Zygoptera, this bridge was necessarily short, but as the base of the wing broadened, the bridge gradually extended proximalwards until it finally arrived at the base of the wing. At first very oblique, it gradually straightened out and finally assumed the same line as the distal part of the anal vein itself, so that it took on the appearance of being part of and the base of that vein. By further branching of this vein, the broad base of the Anisopterous wing has been developed.

Dr. Tillyard also pointed out that the evolution of the hindwing in the Odonata was generally a stage ahead of that of the forewing; arising from this could be explained the Zygopterous nature of the discoidal cell in the forewings of the Anisozygoptera, compared to its Anisopterous nature in the hindwings; thus the Zygoptera were linked up with the Anisoptera.

It will be seen from a perusal of the previous part of this paper, that Dr. Tillyard had abandoned this theory in favour of Carpenter's, but in doing so I feel that he was certainly premature. As I shall try to show, he was quite correct in his original surmise that the Anisoptera had descended from the Zygoptera, although the means, given by him, by which this was accomplished, must be modified in the light of the new evidence now available.

Carpenter's theory:—

This theory seeks to explain that the anal vein in the Anisoptera has

always had an independent origin from the base of the wing, and that its pretracheation is quite as fallacious as Needham's supposed crossing of Rs. The Anisoptera therefore were derived from a type with a broad base to the wings, and in which the anal vein was independent of CuP. Such types he has described from the Permian of Kansas and designated Protanisoptera. The Zygoptera, on the other hand, have the anal vein fused at its base with CuP and are therefore a specialization over the Anisoptera; these, he claims, arose from the Protodonata independently of the Anisoptera and through Protozygopterous types.

Carpenter was undoubtedly correct about the independent origin of the anal vein in the Anisoptera, but, as I shall show, he was quite fallacious in his interpretation of its origin in the Zygoptera. Carpenter in his definition of the Protozygoptera gives: "CuP and IA fused together for the length of the petiole"—(Carpenter, 1931, Amer. J. Sci., 21:115), and again (p. 132, op. cit.): "There can be no doubt, of course, that CuP and IA are fused in *Kennedyia* and *Progoneura* (Protozygoptera)", yet in the same work (p. 112) he says:—"I do not believe that either the tracheation of the nymphs or the data of paleontology have proved that Ac is a portion of the true anal vein IA; on the contrary, for reasons discussed below, I consider the tracheal studies to be as negative as those on the radial sector and the media, and regard the paleontological evidence as positive proof against the accepted understanding of the anal crossing". Therefore I feel, that he, in spite of his interpretations of the course of the anal vein in the Zygoptera, had an intuition that such a solution was not altogether correct.

To these two theories I now add a third and, I hope, a correct one. This new theory seeks to prove that the Anisoptera have, in their descent from the Protodonata, passed through a Zygopterous stage, and that proof of this rests on the evidence afforded by a number of vestigial Zygopterous characters found in present-day Anisoptera. Moreover, it shows that the anal vein arises independently of CuP from the base of the wing in the Zygoptera as well as in the Anisoptera.

In stating my theory, I shall employ the evidence to be obtained from a comparative study of the following five structures in the Odonate wing:—
1.—The primary pair of antenodal nervures. 2.—The cubito-anal cross-vein Ac (anal crossing). 3.—The nodus. 4.—The origins of the two main veins Riv + v and IRiii, and, lastly, 5.—The discoidal cell.

1.—The primary antenodal nervures. (Fig. 1.)

In the costo-antenodal area of any wing belonging to the Anisopterous families Petaluridae, Gomphidae, Cordulegasteridae, Aeshnidae and the more primitive forms of the Libellulidae (*Synthemiopsis* and *Synthemis*, Australia), two robust antenodals are found strongly differentiated from the remaining weaker ones. They are always situated at about the same relative distance from the base and nodus of the wing and from each other. The proximal one of these, save in a few cases, where one or more subcostal basal antenodals have been added, is always the most basal of all the antenodals. If these and their relative positions be compared with a similar pair of antenodals present in all the Zygoptera (except in the more highly developed families Epallagidae and Agriidae), it will be seen that they agree so closely as to leave no doubt that they are homologous and obviously derived from a common ancestor. As they are absent in the Protodonata, it follows that they must have been derived from the Protozygoptera or Protanisoptera. In the former (*Progoneura* and *Sushkinia*), a

pair of antenodals is found occupying the same relative positions as the primaries of present-day genera, but the costal and subcostal portions of these are not in alignment. As we ascend the ladder of evolution, however, as in *Kennedyia* and all succeeding forms of the Coenagriidae, we find these portions have come into alignment and now form the two robust antenodals which we still see in recent genera.

In the Protanisoptera, the evidence of primaries is not nearly so clear. Both Tillyard and Carpenter have fallen into the same error of confusing an oblique vein running from the apex of the precostal area from costa to radius, as the proximal primary antenodal vein but it is far too near the base of the wing, far too oblique and there exists no evidence that it was formed from separate costal and subcostal portions, for it to be the homologue of this vein. In *Ditaxineura* there exist a number of costal and subcostal antenodals, but they are not nearly in alignment; however, there is a possibility that two strong antenodals could be formed from these by subsequent alignment in more highly developed forms succeeding them. In *Polytaxineura* and *Pholidoptilon* the primaries are again doubtfully present; Tillyard gives the 1st, 5th and 6th as the coinciding antenodals; the first of these is, of course, the precostal brace vein, which must be ruled out, and the other two are adjacent to one another and so close together as to differ entirely from the positions of true primaries. Of *Pholidoptilon*, Tillyard has said:—"1st antenodal very oblique and complete, and suggests the brace vein of the Plectoptera". This again is the precostal brace vein and, apart from it, there is only one other coinciding, which occupies the position normally occupied by the distal primary antenodal.

Thus from the poor evidence of primary antenodals in the Protanisoptera and the undoubted evidence of these in the Protozygoptera, as well as the appearance of these vestigial structures in the wings throughout the Anisoptera, the assumption must be that the latter suborder has developed from Zygopterous ancestors.

2.—The cubito-anal cross-vein (anal crossing, Ac). (Part I, Ac in all figures.)

In the cubital space throughout the whole Order Odonata, a short cross-vein is found connecting CuP with the posterior border of the wing, or with the anal vein where this intervenes. It is especially plain in the Coenagrioidae and the Anisoptera, because in them there are no other cross-veins in this space with which to confuse it. (In a small percentage of the Anisoptera, other cross-veins may be present, but as the cubito-anal vein is nearly always the most basal, is nearly always very oblique as compared to the other cross-veins, and also, is usually more robustly built, there is never any difficulty in picking it out.) In the higher forms of the Zygoptera, where many cross-veins often occur in the cubital space, difficulty may be experienced in deciding which is the correct vein, but that it is present, can be proved by comparison with other nearly related species; in genus *Vestalis*, for instance, *V. amoena* is the only species in which the cross-veins in the cubital space are restricted and in which the true cubito-anal cross-vein is isolated; it is difficult to pick out this vein in all other species of *Vestalis*. *There is not the slightest doubt that this vein in the two suborders Zygoptera and Anisoptera is homologous and derived from the same source.* The problem is, how far back have we to look for this latter?; did the vein develop from the Protozygoptera or from the Protanisoptera, or did it antedate both of these?

In the Protodonata (*Protagrion*) the space between the veins CuP and IA is traversed by a great number of undifferentiated cross-veins and there is therefore no evidence of the anal-crossing, Ac.

In the Protozgyoptera, this space is traversed by a single vein which is very long and very oblique. However, by an examination of all the known forms, we are able to see its evolution into a shorter and less oblique structure which is undoubtedly homologous to the cubito-anal cross vein Ac. We thus see that the anal-crossing was already established in the lower Permian and in the Protozgyoptera.

In the Meganisoptera, Lameere pointed out the presence of an oblique vein running between CuP and IA at the base of the wing, which he believed to be homologous to the anal-crossing of the Odonata. Carpenter has since pointed out that this vein is sometimes duplicated and at other times altogether absent, as in *Oligotypus*, so that it cannot be homologous to the vein Ac. I do not think that this point is of much importance to the present problem, since, although the Meganisoptera have descended from the same ancestral Protodonates, they are not necessarily in the direct line of descent of present-day Odonata, that is to say, the Meganisoptera may have branched off from the Protodonata before any reduction of the base of the wing set in, such as we see in the Protozgyoptera.

In the Protanisoptera, cross-veins in the cubital space number from 2 to 5, and most of these are more or less oblique and undifferentiated. One of them, however, stands out rather noticeably from its constant position at or just proximal to the pronounced curve in CuP and IA. It is identical in all known specimens of the Protanisoptera and I am therefore of opinion that it represents the cubital vein Ac. Carpenter points out another cross-vein situated near the base of the wing, but, because it is not constant in its presence, rejects it as homologous to Ac; in any case, it is far too near the base of the wing to be this vein. He is of the further opinion that there is no vein oblique enough or sufficiently differentiated to represent Ac and therefore believes that the anal-crossing is altogether absent in the Protanisoptera. But he has overlooked the fact that Ac is constantly present in all recent species of Anisoptera, so that if it is not an ordinal character in the Protanisoptera, these cannot possibly be the ancestors of the Anisoptera. Thus the very character which he raises to invalidate the Protozgyoptera as the ancestors of the Anisoptera, turns out to be their best advocate. This will be better understood if the true function of Ac be fully realized. This I have explained in a recently published paper dealing with the fallaciousness of the theory of pretracheation (1938, Proc. Roy. Ent. Soc. Lond. 13: 60-70) and which may be briefly reviewed here:

Veins situated on the periphery of the larval odonate wing have no or but poor tracheal supplies, as evidenced by the atrophied condition of the costal trachea and the total absence of tracheation of the base of the anal vein in the primitive Zygoptera. These peripheral veins receive their nourishment from plasma circulating in the wing-case itself.

The anal trachea arises at the same level as its vein, so evidently, at one time, supplied the base of the vein. It would appear that through reduction of the base of the wing, the anal vein was finally brought on to the wing border with which it fused. In such a position it became a peripheral structure and so was rendered independent of its tracheal supply. It might be thought that, in such a position, the anal trachea would have undergone atrophy, as in the case of the costal one, but there is this great

difference between the two veins, for whereas the costa always remains a peripheral structure, and so always remains independent of a tracheal supply, the anal vein, after a short distance, again enters the body of the wing and from then onwards becomes dependent on some trachea for its nourishment. It is just at the point where it enters the body of the wing that the anal trachea abandons the cubitus and turns back to rejoin its own vein; a fine example of the conservatism of Nature! The anal trachea on leaving its vein at the extreme base of the wing runs forward to join CuP and leaves that trachea to rejoin IA by means of the cubito-anal vein. It is because the anal trachea has always employed this cross-vein that Ac has become *fixed* and still exists as an ordinal character. Thus *the presence of this vein Ac in any wing implies that the ancestral type has gone through a stage where the base of the wing was sufficiently reduced as to bring the anal vein on to the border and drive the anal trachea inwards to the cubitus*. Its constant presence in the wings of the Anisozygoptera and Anisoptera is sufficient proof that their ancestral type was one in which the wings were much reduced, as in the Zygoptera.

3.—The Nodus. (Fig. 11, 1 to 4.)

We are so accustomed to regard the nodus as a pseudo-joint or as a simple and useful landmark in the costa, that we have come to regard it as a homogeneous organ, varying but little or not at all in the various families of the Odonata. In its primitive condition, when it is in the making, it certainly shows wider differentiation, but, from the Coenagriidae onwards, it has not been regarded as an organ which shows any variation. Recently I have made an examination of the nodus throughout the various families, and now show the various types which are present. The chief value in this research, as applied to the present paper, is to show that the nodus in the Protanisoptera is almost identical to that found in the primitive Zygoptera, so that both these suborders might have derived their nodus from the same ancestral type, viz., from the Protozygoptera. Carpenter thinks that the nodus in the Protanisoptera is much more highly developed than that of the Protozygoptera, but this is to be expected, if the former have arisen from the latter. It may be argued that, as they are both found occupying the same geological horizon, one cannot have developed from the other, but it must be pointed out that the Coenagriidae have shown remarkably little change from Permian times to the present day, so that there is good reason to believe that they went far back of the Permian; evolution, on the other hand, may have been much accelerated in the case of the Protanisoptera.

In his ancestral type for the Anisozygoptera, Carpenter requires that the nodus should be situated at about the middle of the wing or somewhat more distally. But in many of the higher forms of the Zygoptera (*Epallage*) the nodus is at or near the middle of the wing, and we know that such forms developed from those in which the nodus was situated very proximal. Thus I think that the Anisozygoptera could just as easily have developed from some Zygopterous type.

4.—The origins of Riv + v and IRiii.

In the Protanisoptera the origins of Riv + v and IRiii are at the level of the nodus and distal to it respectively. No intermediate forms are known, either fossil or recent, between them and the Anisozygoptera, and, in the latter, the origins of these two main veins have recessed to about mid-way between the nodus and arculus.

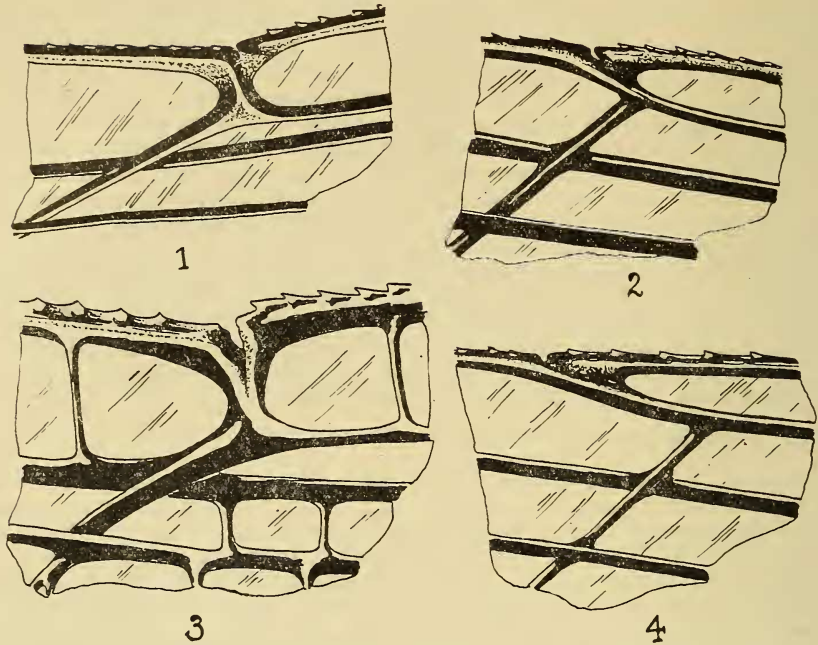


Fig. 11.—The Nodus.—1.—Chlorocyphidae. 2.—Coenagriidae. 3.—Epallagidae. 4.—Protanisoptera. Note the similarity between Figs. 2 and 4, pointing to a common origin for these two suborders.

In the Protozygoptera, the origins of the two veins both lie somewhat distal to the level of the nodus, but as we follow the evolution of their undoubted descendants in the Zygoptera, we are able to follow the recession of these veins step by step until we arrive at a stage quite similar to that found in the Anisozygoptera. *The proximal origin of Riv + and IRiii is basic for the whole of the Anisoptera, as well as for the higher and many lower forms of the Zygoptera*, but we have no evidence that it was so for the Protanisoptera or their earlier descendants, if any.

5.—The Discoidal cell. (Part I, *dc* in all figures.)

The discoidal cell, as a quadrangular space, open at the base, is similar in the Protozygoptera and Protanisoptera. In the former, however, we find it becoming acutely pointed distally in at least one species (*Permolestes gracilis* Martyn.), and it is so for the greater part of the primitive Zygoptera right up to the Megapodagriidae.

In the Anisozygoptera, the discoidal cell of the forewing is of this same character, but that of the hindwing is a stage in advance and has taken on Anisopterous characters, that is to say, although originally typically Zygopterous in shape, it has evolved into one similar to that found in the Anisoptera. There is no evidence to show that the Protanisoptera developed a Zygopterous discoidal cell from which the Anisozygopterous, dimorphic one, could have developed; on the other hand, that for the Protozygoptera could not be more convincing.

It will be seen that the total evidence is overwhelmingly in favour of the Protozygoptera being the true ancestors of the Anisozygoptera and so, of the Anisoptera. Discarding all other evidence save that of the cubito-anal vein Ac, the presence of this in the wings of all Anisoptera is quite meaningless unless we presume for them an ancestor with an extremely reduced and petiolate wing.

In the third and final Part of this paper I shall deal with the Sub-orders Anisozygoptera and Anisoptera.

(To be continued.)

ADDENDA ET CORRIGENDA TO PART I.

- 126, line 25.—After "Part", insert a comma.
 128, line 2.—For "another" read "anterior".
 130, line 6.—For "wide-" read "wing-".
 line 19.—For "(AP)" read "(AxP)".
 133, legend to Fig. 5.—for "schucheri" read "schucherti".
 132, line 3 in footnote.—For "agle" read "angle".
 134, line 21.—For "On" read "In".
 141, line 19.—For "*Palaeothemis* Mart." read "*Permothemis* Mart." The name *Palaeothemis* is preoccupied by *Palaeothemis tillyardi* Fras., in Anisoptera, and the new name was therefore proposed by Martynov, 1935. We greatly regret to report the recent death of this great Russian palaeontologist who was a close collaborator with Dr. Tillyard.
 line 8 from bottom of page.—For "Odonatoid" read "Odonatoid".
 142, line 4.—"*Palaeothemis*" correct as for above.
 line 22.—For "CuP" substitute "posterior border of wing".
 144, line 17.—For "CuP" read "IA" and for "IA" read "the posterior border of wing".
 line 24.—For "IA" read "Ac".
 148, line 18.—For "Archizygoptera" read "Lestoidea".
 149, line 7 of footnote.—For "nervure IA" read "anal trachea".
 152, line 11 from bottom of page.—After "or" insert "IA".
 163, line 3 of second paragraph.—After "antenodals" insert "except in *Isosticta*".
 165, line 15 from bottom of page.—For "subcoidal" read "subdiscoidal".
 166, line 3.—For "Onychoargia" read "Onychargia".
 167, line 4 in explanation of text-figures.—For "Se" read "Sc".
 line 16.—Delete "for"
 168, line 8.—For "Ayi" read "Axi".